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Smart, Christopher

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Holocene variations in North Atlantic export productivity as reflected in bathyal benthic foraminifera

Christopher W. Smart [a*], Ellen Thomas [b,c] and Curtis M. Bracher [a]

[a] School of Geography, Earth and Environmental Sciences, University of Plymouth, Drake Circus, Plymouth, Devon, PL4 8AA, UK

[b] Department of Geology and Geophysics, Yale University, 210 Whitney Avenue, New Haven, CT 06520–8109, USA

[c] Department of Earth and Environmental Sciences, 265 Church Street, Wesleyan University, Middletown, CT 06459, USA

* Corresponding author

Abstract

The subpolar NE Atlantic Ocean experiences seasonal fluxes of labile organic matter (phytodetritus) which are expected to strongly influence the composition of benthic foraminiferal assemblages and benthic foraminiferal accumulation rates. We studied export production over the last 12 kyr at a sampling resolution of approximately 250-300 years through an investigation of bathyal benthic foraminiferal assemblages (>63 µm) at Ocean Drilling Program (ODP) Site 980 on the Feni Drift (55°29'N, 14°42'W, 2179 m water depth).

During the last 12 kyr, faunas at Site 980 were dominated (~75%) by *Cassidulina obtusa, Nonionella iridea, Bolivina difformis, Trifarina pauperata, Alabaminella weddellensis, Stainforthia fusiformis, Cassidulina laevigata* and *Eilohedra vitrea*. The absolute and relative abundances and diversity of these and other species varied significantly. In the interval ~12-10 ka, *A. weddellensis, S. fusiformis* and *T. pauperata* had higher % abundance (named here 'H10 species'), but this is not reflected in a higher accumulation rate, suggesting that surface productivity was low, at highly variable conditions. Species at lower % abundance during this time include *B. difformis, C. laevigata, C. obtusa, E. vitrea* and *N. iridea* (so-called 'L10 species'). The '8.2 ka cold event' was characterized by increased carbonate dissolution (reflected in decreases in the absolute abundance, benthic foraminifera accumulation rate, weight % coarse fraction, and presence of poorly preserved/fragmented benthic foraminifera). Peaks in the relative abundance of species which, in our opinion, exploited phytodetritus ('phytodetritus species': *N. iridea, A. weddellensis, C. obtusa*, and rare *Epistominella exigua*) occurred at 8.0 ka, 7.0 ka, 6.3-5.6 ka, 4.7 ka, 4.3-3.4 ka and 2.4 ka. These peaks generally correspond to peaks in absolute abundance (number of specimens per gram, accumulation rate), indicating increases in the seasonality of export productivity. However, the 'phytodetritus species' do not covary in absolute and relative abundance over the studied interval, suggesting that they have somewhat different ecological requirements.

There appears to be no simple relationship between changes in the degree of seasonality of export productivity (i.e., abundance of ‘phytodetritus species’) and records of palaeoclimatic/palaeoceanographic proxies, suggesting that bentho-pelagic coupling (arrival of food on the seafloor with local surface productivity) might not have been straightforward in this region. Site 980 is located in the hydrodynamically active area of Feni Drift, and during the Holocene, currents might have winnowed and removed fine-grained organic matter, making it unavailable to benthic organisms. Alternatively, there may have been changes in remineralization and/or mid-water competition for food, so that the fraction of the organic flux that reached the seafloor may have varied. Holocene benthic foraminiferal assemblages thus reflect highly dynamic conditions in export productivity and arrival of organic matter at the seafloor.

Keywords: Bentho-pelagic coupling; seasonality of productivity; phytodetritus species

1. Introduction

The Holocene (the last 11.7 kyr) saw relative climate stability compared to the last glacial period, although significant Holocene climate change occurred (e.g. Mayewski et al., 2004; Wanner et al., 2008, 2011, 2015). The Holocene Thermal Maximum, due to orbital forcing, was followed by progressive cooling starting at ~5-4 ka (Renssen et al., 2012; Marcott et al., 2013; Wanner et al., 2008, 2015). Superimposed on this long-term trend there were (8-10) multi-decadal- to century-scale ice-rafting maxima (the so-called Bond cycles), by some interpreted as cooling events (Bond et al., 1997, 2001; Mayewski et al., 2004; Wanner et al. 2011, 2015). There has been considerable discussion whether these Holocene cycles had periodicities of ~1500 years, and whether they were global. They might have been largely restricted to the North Atlantic and surrounding areas (e.g. Wanner and Bütikofer, 2008; Wanner et al., 2015), but potentially linked, coeval cooling events have been reported in Asia, North America and the Pacific Ocean (e.g. Goswami et al., 2006; Isono et al., 2009; Wanner et al., 2011, 2015). Suggested causes of the Bond cycles include solar irradiance changes, volcanic eruptions, changes in ocean meridional overturning circulation, and variations internal to the climate system (see Wanner et al., 2011, 2015). However, to complicate matters, there is no consensus whether the Bond cycles actually exist, with some suggesting that they are an artefact of under-sampling annual cycles (Wunsch, 2000), and others (e.g. Wanner et al. 2008; Obrochta et al., 2012) questioning their ubiquity, as well as their exact timing and periodicity.

A great range of proxies are used to document various aspects of climate variability. Benthic foraminifera are an important component of modern ocean floor communities (e.g. Gooday et al., 1992; Gooday, 1999, 2003), and their distribution, diversity and species abundance in the fossil record have been used extensively as palaeoceanographic proxies (for reviews see Smart, 2002; Gooday, 2003; Jorissen et al., 2007; Gooday and Jorissen, 2012). Complex factors control the abundance and microhabitat distribution of benthic foraminifera, but it is generally accepted that the flux of organic matter and bottom and pore water oxygen concentrations are the major controlling variables in the food-limited deep-sea

environments (e.g., van der Zwaan et al., 1999; Jorissen et al., 1995, 2007). Additional factors such as bottom water hydrodynamics, carbonate saturation, and temperature may be important in specific settings (e.g. Bremer and Lohmann, 1982; Mackensen et al., 1995; Murray, 2001; Schönfeld, 2002; Jorissen et al., 2007; Rasmussen and Thomsen, 2017).

The flux of organic matter (food) from the euphotic zone to the deep ocean floor exerts a strong influence on the abundance, diversity and biomass of all deep-sea benthic organisms (e.g., Rowe, 1983, Gage and Tyler, 1991), including benthic foraminifera (e.g., Herguera and Berger, 1991; Altenbach et al., 1999, Gooday, 2003). Benthic foraminifera show resource partitioning, i.e., they use different types of food in a non-competitive way (Murray, 2006). Their assemblage composition may be related to both the amount and quality of organic matter (e.g. Caralp, 1989; Altenbach et al., 1999; Fontanier et al., 2005), and whether or not the supply is seasonal or otherwise intermittent (Loubere and Fariduddin 1999; Sun et al., 2006). Labile organic matter (phytodetritus) is delivered to the sea floor in seasonal pulses in many mid-latitude areas (e.g. Billett et al., 1983; Rice et al., 1994; Smith et al., 1996), and phytodetritus abundance strongly influences the composition of benthic assemblages, including foraminifera (e.g., Gooday, 1988, 1996; Gooday and Turley 1990; Ohga and Kitazato, 1997; Kitazato et al., 2000). This is particularly evident in the NE Atlantic, where some species of opportunistic benthic foraminifera respond rapidly to the presence of phytodetritus by feeding on the detritus, reproducing rapidly and building up large populations (e.g. Gooday 1988, 1993, 1996).

In the abyssal NE Atlantic, where the overall flux of organic matter to the seafloor is fairly low despite high surface productivity, the ‘phytodetritus species’ are dominated by *Epistominella exigua* and *Alabaminella weddellensis* (e.g. Gooday 1988, 1993, 1996; Smart and Gooday, 1997). The abundance of these ‘phytodetritus species’ has been used to document variability in seasonally pulsed organic matter inputs across periods of climate change (e.g., deglaciation) (e.g., Smart et al., 1994, 2010; Thomas et al., 1995; Thomas and Gooday, 1996; Nees et al., 1997; Nees and Struck, 1999; Smart, 2008; Diz and Barker, 2016).

In the bathyal NE Atlantic, where the overall annual delivery of organic matter to the sea floor is higher (Fig. 1), the 'phytodetritus species' may be dominated by *Nonionella iridea, A. weddellensis* (*Eponides pusillus* of Gooday and Hughes, 2002) and *Cassidulina obtusa* (Gooday and Lambshead 1989; Mackensen et al., 1990; Lambshead and Gooday, 1990; Gooday and Hughes, 2002; Duchemin et al., 2005, 2008). *Nonionella iridea* is associated with fresh phytodetritus in many regions (i.e., has green protoplasm even outside the photic zone) (Murray, 2006). The species responds opportunistically to phytodetritus (Gooday and Hughes, 2002; Duchemin et al., 2005, 2008; Alve, 2010), although evidence from experimental work and sediment data from the upper bathyal of Oslofjord, Norway indicate that it has its peak abundance in seasons without active deposition. The species may be linked more to refractory degraded organic matter and associated bacteria and other microbes rather than to fresh phytodetritus (Duffield et al., 2014, 2015). *N. iridea* may live in areas of active phytodetritus deposition, but in the upper, suboxic sediments below the actual phytodetritus layer (Murray, 2006).

Stainforthia fusiformis is an opportunistic species and its abundance most likely reflects highly variable environmental conditions (Alve, 2003; Murray, 2006). It has been associated with physically disturbed sediment (Alve and Murray, 1997), low oxygen shelf and slope areas, hydrographic frontal regions (Scott et al., 2003), and availability of refractory, degraded organic matter (Duffield et al., 2015).

Assemblage composition as well as benthic foraminiferal accumulation rates (BFARs) have been suggested to be a proxy for palaeoproductivity (e.g. Herguera and Berger, 1991), because benthic assemblages depend on the food flux from surface productivity. However, factors such as calibration, changes in remineralization rate of organic matter in the water column, oxygen levels, dissolution and taphonomic effects limit the use of BFAR in a quantitative sense (e.g., Jorissen et al., 2007). Only a very small (generally <1%) percentage of organic matter reaches the deep sea floor (e.g., Martin et al., 1987), so surface ocean and chemical and biological water-column processes materially affect the flux of organic material reaching the benthos. The amount of organic matter exported from the photic zone, first to the bottom of the mixed layer and then on to the sea floor, varies strongly with pelagic ecosystem composition,

and with the abundance of mid-water biota, so that climatic changes affecting these systems also affect the benthos (e.g., Thomas et al., 1995; Henson et al., 2012, Arndt et al., 2013). Furthermore, in hydrodynamically active regions (such as the drift setting of Site 980), phytodetritus is not simply transported vertically from surface to bottom, but may be deflected laterally, and/or concentrated in some areas (e.g., Murray, 2006), depending upon sea floor topography (Arreguin-Rodriguez et al., 2016) and current activity. Fine grained, low-density organic material may be winnowed by bottom currents, thus removed from availability for the benthos, and refractory organic matter is laterally transported, affecting BFAR as well as the abundance of such taxa as the high-food depending bolivinids. High abundances of bolivinids have been associated with high fluxes of laterally transported refractory organic matter in the present Bay of Biscay (Hess and Jorissen, 2009) and in the Oligocene Fuente Caldera section (Spain) (Fenero et al., 2012).

In general, at a location such as Site 980, located in the hydrodynamically active area of Feni Drift, environmental factors other than vertical organic matter fluxes from surface productivity in the directly overlying waters may have been important for Holocene benthic foraminiferal faunas. Bentho-pelagic coupling may not have been straightforward, with a correlation between primary productivity and arrival of food to the seafloor not a simple logarithmical correlation function (Martin et al., 1987; Arndt et al., 2013). Both assemblage composition and BFARs should be considered as proxies for arrival of organic matter at the seafloor, i.e., reflecting some combination of export and primary productivity influenced by water column processes, and we must keep this in mind while interpreting our faunal records for Site 980.

The main aim of this study is to document the relationship between Holocene changes in the degree of seasonality of export productivity (i.e., abundance of ‘phytodetritus species’) at bathyal North Atlantic ODP Site 980 (55ºN, 14º42’W, 2179 m water depth), and compare it with published palaeoclimatic/ palaeoceanographic records at the same site, and with faunal records at other sites in the same general area (Thomas et al., 1995; Smart 2008).

2. Site location and oceanography

The sediments for this study were sampled in cores from Ocean Drilling Program (ODP) Site 980 (Hole 980B) on the Feni Drift, subpolar northeastern Atlantic Ocean (55º29'N, 14º42'W, 2179 m water depth) (Fig. 1). This site has been the subject of extensive investigations of Quaternary palaeoceanography and palaeoclimatology (e.g., McManus et al., 1999; Oppo et al., 1998, 2003, 2006, Benway et al., 2010, Stolz and Baumann, 2010). Today, surface waters at Site 980 lie in the path of the North Atlantic Current (NAC), which transports warm Gulf Stream water poleward (Fig. 1a). The North Atlantic subpolar gyre (SPG) occurs to the north of the area and the subtropical gyre (STG) lies to its south (Fig. 1a), with the Arctic Front (AF, the boundary separating the Arctic and Atlantic domains) lying near Greenland (Swift and Aagaard, 1981). During cold events of the last interglacial (MIS5), the SPG weakened and the AF may have reached Site 980 (Mokeddem et al., 2014).

Deep waters at Site 980 are dominated by North Atlantic Deep Water (NADW), largely comprising Labrador Sea Water (LSW) with a small component of Iceland-Scotland Overflow Water (ISOW) (Fig. 1a). The NADW in this area has lower oxygen concentrations than newly ventilated waters, due to the presence of relatively poorly ventilated, southerly derived Eastern Basin Deep Water (EBDW), comprising recirculated NADW (Curry et al., 1988) and Southern Ocean Water (SOW) (Lonsdale and Hollister, 1979).

During glacial and deglacial times, the deep waters contained a combination of northerly and southerly derived waters, with NADW replaced by the more shallow water mass named Glacial North Atlantic Intermediate Water (GNAIW; e.g., Oppo and Lehman, 1993; McManus et al., 1999, Howe et al., 2016, Menviel et al., 2016). Reductions in northern-derived deep waters may have been associated with the presence of poorly ventilated EBDW (Oppo et al., 2006). Alternatively, both the northerly and the southerly sourced deep waters may have been reduced in volume, leading to a generally more poorly

ventilated Atlantic basin (Menviel et al., 2016). During the Holocene, NADW volume varied on centennial to millennial time scales, with reductions of NADW occurring at 9.3 ka, 8.0 ka, 5.0 ka and 2.8 ka (Oppo et al., 2003).

Present average annual primary production estimates in the area, calculated using the Vertically Generalized Production Model (VGPM; Behrenfeld and Falkowski, 1997a,b) and SeaWiFS phytoplankton chlorophyll concentrations (Sun et al., 2006, fig. 3a; Corliss et al., 2009, fig. 1A), are in the range 200-225 g C m^{-2} yr^{-1} (Fig. 1a). The area experiences strongly seasonal inputs of phytodetritus during the late spring/early summer, which exert a strong influence on benthic organisms, including benthic foraminifera (Gooday and Lambshead, 1989; Gooday and Hughes, 2002). The location of high phytodetritus productivity, however, varied from the last glacial maximum to today, with northward motion of the zone of highest productivity during deglaciation (Thomas et al., 1995; Nees et al., 1997).

3. Chronology of ODP Hole 980B

Age control for ODP Hole 980B is provided by monospecific planktic foraminifera accelerator mass spectrometry (AMS) ^{14}C dates (Oppo et al., 2003), as recalibrated by Benway et al. (2010). Sample ages were interpolated from Benway et al. (2010), and updated ages have been calculated for the oxygen and carbon benthic foraminiferal isotope records of the 1.27-10.07 kyr interval (Oppo et al. 2003) and 10.11-11.96 kyr interval (Oppo et al., 2007) (Fig. 2). There are radiocarbon age reversals in the upper 5 cm of the core (Oppo et al., 2013), so only data for samples older than 1.27 kyr (0.360 metres composite depth) are considered and plotted (Fig. 2). Therefore, the ages of the two youngest samples in our study (at 0.045 mcd = 0.78 kyr and 0.155 mcd = 0.95 kyr) should be considered with caution. The differences in calendar ages between ages in Oppo et al. (2003) and those in Benway et al. (2010) are generally small for the interval 0.64-11.70 kyr (mean -0.054 kyr, n = 15). The sedimentation rates for the 1.27-11.66 kyr interval vary from 5.4 to 72.5 cm kyr^{-1} (mean 47.5 cm kyr^{-1}, n = 122) (Fig. 3b).

4. Material and methods

A total of 44 sediment samples from the 0.78-11.66 kyr interval were studied from ODP Hole 980B, corresponding to a sampling resolution of approximately 250-300 years. The samples were dried, weighed and soaked in a 10% Calgon solution (sodium hexametaphosphate) to disaggregate the sediment. The samples were washed through a >63 µm sieve, then dried and weighed. Wherever possible, >250 specimens of benthic foraminifera from each sample were picked and identified to species level in the >63 µm size-fraction. The number of specimens per gram of dry bulk sediment (NPG) were calculated. In general, more than 200 specimens of benthic foraminifera per sample are needed to represent species diversity for Neogene assemblages (Thomas, 1985). Benthic foraminiferal species names follow the World Foraminifera Database (Hayward et al., 2018), and counts for studied samples are provided in the Supplementary material.

No dry bulk density (DBD) data are available for the calculation of accumulation rates (number of specimens cm^{-2} kyr^{-1}), so wet bulk density (WBD) data obtained by gamma-ray attenuation were used (Jansen et al., 2005; see also Stolz and Baumann, 2010). The accumulation rates (AR) of benthic foraminifera (>63 µm) (BFAR) were calculated as: number of specimens per gram of dry bulk sediment x linear sedimentation rate (cm/kyr) x WBD (g/cm^3).

In order to compare our BFAR data with those available from other sites, we must estimate the BFARs as based on DBD. In Hole 980A (also drilled at Site 980), some low resolution WBD and DBD data are available (Jansen et al., 1996, table 19). In samples 980A-1H-1, 75-77 cm (0.75 mbsf) and 980A-1H-2, 75-77 cm (2.25 mbsf) the WBD is 1.500 g/cm^3 and 1.521 g/cm^3 respectively and the DBD is 0.761 g/cm^3 and 0.789 g/cm^3 respectively (Jansen et al., 1996, table 19). Using the mean of this basic relationship (i.e., 1 g/cm^3 WBD = 0.513 g/cm^3 DBD), we tentatively estimated the DBD, and therefore

BFARs, for our samples. This results in an overall halving of the BFAR values compared with BFARs calculated using WBD.

Data on benthic foraminiferal NPG, AR and % coarse fraction (>63 µm) are provided for all samples (Supplementary material). Some samples (at 0.045 mcd [0.78 ka], 0.155 mcd [0.95 ka], 0.525 mcd [2.06 ka], 1.735 mcd [8.16 ka], 1.785 mcd [8.45 ka], 1.825 mcd [8.69 ka], 2.225 mcd [10.25 ka]) contained no or very few benthic foraminifera (0-13 specimens) (Table 1) thus were excluded from the percentage and diversity calculations. For each sample, the diversity was recorded in terms of the Fisher's alpha index (Fisher et al., 1943). The percentage of planktic foraminiferal fragments in the >63 µm size-fraction (calculated as the percentage of planktic foraminiferal test fragments relative to whole planktic foraminifera plus test fragments on total counts of >300 specimens), and the percentage of benthic foraminifera in the >63 µm size-fraction relative to the total foraminiferal assemblage (benthic + planktic) were also recorded.

'Phytodetritus species' (associated with seasonally pulsed organic matter fluxes) are defined as the combined percentages of *Cassidulina obtusa*, *Nonionella iridea*, *Alabaminella weddellensis* and *Epistominella exigua* (e.g. Gooday 1988; Thomas et al., 1995; Gooday and Hughes, 2002; Smart, 2008). 'High food species' (associated with sustained organic matter fluxes) are defined as the % sum of *Abditodentrix* spp., *Bolivina* spp., *Bolivinellina* spp., *Brizalina* spp., *Bulimina* spp., *Globobulimina* spp., *Melonis* spp., *Stainforthia* spp., *Trifarina pauperata* and *Uvigerina* spp. (e.g. Lutze and Coulbourn, 1984; Altenbach et al., 1999).

In order to identify groupings of species, a Principal Components Analysis (PCA) with VARIMAX rotation was performed on the percentage species data and two datasets were considered (n = 37). First, the percentage data was reduced to include species that were present in at least three samples and percentages were >2% in at least one sample. This resulted in 30 species, but the Kaiser-Meyer-Olkin (KMO) Measure of Sampling Adequacy value was 0.391, which is considered unacceptable (e.g. Dziuban and Shirkey,

1974; Cerny and Kaiser, 1977). Second, the percentage data was reduced to include the top 23 ranked species with percentages of >0.5% of the total, resulting in an unacceptable KMO value of 0.368 (e.g. Dziuban and Shirkey, 1974; Cerny and Kaiser, 1977). Given these results, we decided not to pursue PCA for interpreting the dataset.

5. Results

The % coarse fraction (>63 μm) is dominated by planktic foraminifera (+ fragments), benthic foraminifera, and occasional radiolarians and sponge spicules (Fig. 3). The % coarse fraction is usually <6% by weight, with strong fluctuations between 7.7 kyr and 12 kyr (Fig. 3c). The % planktic foraminiferal fragments (>63 μm) varied over the last 12 kyr (mean = 36.0%, n = 37) with peaks in fragmentation at 7.7 ka and 9.3 ka (Fig. 3c). The interval <2 ka is not considered because no planktic foraminifera (or fragments) were recorded.

The benthic foraminifera are dominated by calcareous species, mostly well preserved and, in most samples, without apparent signs of dissolution or shell breakage. However, samples with poorly preserved and fragmented benthic foraminifera occur in the interval deposited between 8.5-8.2 ka, and samples with some poorly preserved/fragmented benthic foraminifera at 10.3, 9.3 and 7.7 ka. The % benthic foraminifera (of total foraminifera) fluctuated between ~20% and 0% over the last 12 kyr (Fig. 3e). The top 10 ranked benthic foraminiferal species (by relative abundance), based on the total number of all species present in all 44 samples, are given in Table 2.

Abundance and diversity information is presented in Fig. 4. Diversity (Fisher's alpha index) fluctuated over the last 12 kyr ,with an overall trend towards lower values (Fig. 4h), and with higher values between 11.7-7.7 ka than between 7.6-2 ka. The diversity values are negatively correlated with BFAR, the AR of 'phytodetritus species', and % 'phytodetritus species' (Table 3). In other words, when diversity is higher, BFARs (total) and AR and % of 'phytodetritus species' are low (lower diversity at high

phytodetritus abundance), as also observed elsewhere, e.g. on Shatksy Rise in the Pacific (Ohkushi et al., 2000).

The absolute abundances (numbers of specimens per gram, NPG) and benthic foraminiferal accumulation rates (number of specimens cm^{-2} kyr^{-1}, BFAR) fluctuated strongly over the last 12 kyr (Fig. 4a, e). The fluctuations in NPG and BFAR are very similar. Peaks in BFARs (>200,000 cm^{-2} kyr^{-1}) occurred at 10.0 ka, 9.0 ka, 7.0 ka, 5.9-5.3 ka and 4.0-3.7 ka (Fig. 4e). There are significant positive correlations between the % coarse fraction and NPG and BFAR, but not with % benthics or % planktic foraminiferal fragments (Table 3). There are positive correlations between the % benthics and NPG, BFAR, but not with % planktic foraminiferal fragments (Table 3).

We use the sum in relative abundance of *N. iridea*, *A. weddellensis*, *C. obtusa* (and rare *E. exigua*) as 'phytodetritus species' (mean 41.5%). The 'phytodetritus species' fluctuated between ~12 kyr and ~2 kyr with a general trend towards higher percentages (from ~25% to ~50%) peaking at around ~ 3.8 ka (Fig. 4c). Peaks in the % 'phytodetritus species' (>45%) occurred at 8.0-7.9 ka, 7.0 ka, 6.3-5.6 ka, 4.7 ka, 4.3-3.4 ka and 2.4 ka (Fig. 4c). The % 'phytodetritus species' shows a significant positive correlation with % coarse fraction, and is weakly positively correlated with % planktic foraminiferal fragments and % benthics (Table 3). *Epistominella exigua* constitutes a very small proportion of the 'phytodetritus species', with abundances of <2% between 11.7 and 9.6 kyr, and it is absent between 9.3 kyr and 2.2 kyr. The relative abundances of *C. obtusa*, *N. iridea* and *A. weddellensis* do not covary throughout the studied interval (Fig. 4d), and the patterns in their absolute abundances (NPG and AR) are very similar to those in the NPG and AR of total foraminifera. Also, the NPG and AR of 'phytodetritus species' and the NPG and AR of foraminifera calculated on a 'phytodetritus species'-free basis show very similar trends, and are strongly positively correlated (Table 4). Both the NPG and AR of 'phytodetritus species' are significantly correlated with the % coarse fraction (Table 3).

The percentage fluctuations of the most common benthic foraminifera (each comprising a mean of >5% in all samples throughout the studied interval) are shown in Fig. 5, and their AR in Fig. 6. The relative abundance of *C. obtusa* increased over the last 12 kyr from ~10% to ~40% (Fig. 5a). The relative abundance of *N. iridea* fluctuated from ~2% to ~20% (Fig. 5b). The abundance of *B. difformis* fluctuated over the last 12 kyr, with an overall decrease from 6.7 kyr (16.6%) to 2.2 kyr (7.2%) (Fig. 5c). The percentage of *T. pauperata* fluctuated (~11-1%) with peaks at 10.6 ka (15.1%) and 11.3 ka (12.3 %) (Fig. 5d). The relative abundance of *A. weddellensis* fluctuated, with higher abundances between 11.7-10 kyr, and values increased from ~2% to 6% from 7.7-2.2 kyr (Fig. 5e). The relative abundance of *S. fusiformis* fluctuated, and decreased from ~20% to ~5% over the last 12 kyr with higher abundances at 11.7-10.8 ka (Fig. 5f). The abundance of *C. laevigata* increased over the last 12 kyr from 0-2% to ~9% (Fig. 5g). *E. vitrea* had abundances of <12% throughout the studied interval (Fig. 5h).

Three common species (*A. weddellensis*, *S. fusiformis* and *T. pauperata*) show overall higher relative abundance in the early part of the record (>10 ka), where BFAR is low; we call these the 'H10 species' (i.e. species with higher % abundance before 10 ka). Their combined percentages are ~20-30% from 11.7-10.6 kyr, ~20-6% from 10-2.2 kyr (Fig. 7a). Five common species (*B. difformis*, *C. laevigata*, *C. obtusa*, *E. vitrea* and *N. iridea*,) show overall higher relative abundance in the later part of the record (<10 ka); we call these the 'L10 species' (i.e. species with lower % abundance before 10 ka). Their combined percentages are ~20-30% from 11.7-10.6 kyr and 50-70% from 10-2.2 kyr (Fig. 7b). The AR of both 'H10 species' and 'L10 species' were low before 10 ka (Fig. 7c, d), when overall BFARs were also low. The general fluctuations of NPG and AR of all species, including the 'H10 species' and 'L10 species', are very similar to the variations of NPG and AR of total foraminifera.

The relative abundance of 'high food species' (combined % of *Abditodentrix* spp., *Bolivina* spp., *Bolivinellina* spp., *Brizalina* spp., *Bulimina* spp., *Globobulimina* spp., *Melonis* spp. *Stainforthia* spp., *T. pauperata* and *Uvigerina* spp.) fluctuated between ~20-35% over the studied interval (Fig. 8b). There is no significant correlation between the % of 'high food species' and BFARs (Fig. 8, Table 3). The percentage

of 'high food species', calculated on a 'phytodetritus species'-free basis, fluctuated over the studied interval, but a general trend towards higher values in the interval 11.7-6.7 kyr and lower values in the interval 6.3-2.2 kyr (although variable) is evident (Fig. 8c).

6. Discussion

At bathyal ODP Site 980, NE Atlantic Ocean the absolute and relative abundances, accumulation rates, and diversity of benthic foraminifera fluctuated significantly during the last 12 kyr. The faunas were dominated (~75%) by *C. obtusa*, *N. iridea*, *B. difformis*, *T. pauperata*, *A. weddellensis*, *S. fusiformis*, *C. laevigata* and *E. vitrea*. In the interval before 10 ka, common species with higher % abundance included *A. weddellensis*, *S. fusiformis* and *T. pauperata* ('H10 species'), and common species with lower % abundance are represented by *B. difformis*, *C. laevigata*, *C. obtusa*, *E. vitrea* and *N. iridea* ('L10 species'). This intervals is marked by low BFARs, suggesting that export productivity overall was low. The high abundance of the opportunistic species *S. fusiformis* indicates potentially highly variable bottom conditions.

The species composition and abundance of benthic foraminifera are very similar to those of modern faunas described at nearby BENBO Site C (57ºN,12ºW, 1913-1980 m water depth, Gooday and Hughes, 2002), although, according to SeaWiFS phytoplankton chlorophyll concentrations (Sun et al., 2006, fig. 3a; Corliss et al., 2009, fig. 1A), productivity presently is slightly higher at BENBO Site C (225-275 g C m-2 yr-1) than at Site 980 (200-225 g C m^{-2} yr^{-1}) (Fig. 1). At the BENBO C site, two 'phytodetritus species' (*Nonionella iridea* and *Eponides pusillus* [= *A. weddellensis* of this study]) were common in 'live' and 'dead' assemblages. *Cassidulina obtusa* was abundant, but mainly in the 'dead' assemblages, possibly because its main period of test production occurred after the July sampling period (Gooday and Hughes, 2002). In the 'live' (stained) assemblages, *N. iridea* increased from 5.6% to 20.4% and *E. pusillus* from 1.4% to 11.0% from May (no phytodetritus) to July (phytodetritus present), demonstrating the close link

between phytodetritus deposition and the abundance of these species (Gooday and Hughes, 2002). The 'dead' (unstained) assemblages were dominated by calcareous species, with *N. iridea*, *C. obtusa* and *E. pusillus* as first, second and third ranked species in abundance in the May and July samples (Gooday and Hughes, 2002). The combined percentages of these species were slightly lower in the May samples (44.6-46.7%) than in the July samples (48.8-48.9%). Removing agglutinated species with low preservation potential, the combined abundance of these three 'phytodetritus species' is >45% in the 'dead' assemblage (Gooday and Hughes, 2002, table 6).

The peaks in the % 'phytodetritus species' in our Site 980 record (>45%) at 8.0 ka, 7.0 ka, 6.3-5.6 ka, 4.7 ka, 4.3-3.4 ka and 2.4 ka (Fig. 4f), correspond to increases in the AR of 'phytodetritus species'. These peaks could reflect increases in the seasonality of productivity, i.e., the difference in productivity between, e.g., spring-fall or winter-summer increases (even at the same overall annual productivity), so that more organic matter falls in less time, and/or the productivity during the spring bloom increased. However, the situation is almost certainly more complex, because these opportunistic 'phytodetritus species' do not covary over the study interval, probably indicating that they have somewhat different ecological requirements and preferences for type of/degree of seasonality of phytodetritus: *E. pusillus* occurred physically embedded in phytodetritus, whereas *N. iridea* occurred in the sediment surrounded by an agglutinated cyst (Gooday and Hughes, 2002).

The lack of covariance in abundance between two well-known 'phytodetritus species', *E. exigua* and *A. weddellensis*, has been associated with different ecological requirements and preferences for type of/degree of seasonality of phytodetritus (e.g. Thomas et al., 1995; Yasuda, 1997; Nees and Struck 1999, Ohkushi et al. 2000, Smart, 2008). King et al. (1998) demonstrated that *A. weddellensis* was more common than *E. exigua* in dense, laminated diatom mats in the Neogene equatorial Pacific. Also, *E. exigua* has been described as more related to areas of high seasonality, whereas *A. weddellensis* is more associated with regions of higher productivity (Fariduddin and Loubere, 1997; Sun et al., 2006). In our data, the relative

abundance of this species also appears to be related to high % of 'high food species' (although not high AR of these taxa) in the interval older than 10 ka.

Eilohedra vitrea (= *Epistominella vitrea*), which is common at Site 980, has been linked to high productivity areas with seasonal inputs of organic material (e.g. Alve and Bernhard, 1995; Duchemin et al., 2007; Phipps et al., 2012). In addition, an assemblage comprising the opportunistic species, *N. iridea* and *E. vitrea* was more related to pulsed seasonal food supply than temperature over the last glacial in the central North Atlantic (Rasmussen and Thomsen, 2017). At Site 980, the correlation between the % *E. vitrea* and % 'phytodetritus species' is not significant (Table 4), although there is a good correspondence of fluctuations in the AR of *E. vitrea* and the AR of 'phytodetritus species'. *Bolivina difformis,* which is also common at Site 980, was found to peak only after the spring bloom in the North Atlantic (550 m water depth, Bay of Biscay), suggesting it prefers to feed on material typical of spring blooms (e.g. diatoms, coccolithophores, and other microalgae) (Fernandez et al., 1995; Fontanier et al., 2003). Like *E. vitrea*, the correlation between the % *B. difformis* and % 'phytodetritus species' is not strongly significant ($r = 0.067$, $p = 0.692$, n = 37) (Table 4), but there is a good correspondence of increases and decreases in the AR of *E. vitrea* and the AR of 'phytodetritus species' throughout the Holocene. In bathyal areas (e.g. Sagami Bay, Japan) other bolivinid species (*Bolivina pacifica*) have been linked to seasonal fluxes of organic matter (Ohga and Kitazato, 1997), but lateral transport of more refractory material (as described above)may have affected the abundance of this species.

The significant correlations between NPG and BFARs and the dissolution proxy, % coarse fraction (e.g. Volbers and Henrich, 2002), suggests that dissolution might have affected the abundances of foraminifera at ODP Site 980, but this seems rather unlikely because most samples contain well preserved, non-fragmented benthic foraminiferal specimens. The % coarse fraction is a reliable dissolution proxy only if the ratio between nannofossils and microfossils remains constant through time (Volbers and Henrich, 2002). Coccolith AR at ODP Site 980 were high and relatively stable during the Holocene, with the highest AR in the early and late Holocene (Berger et al., 2014). Coccolith AR and BFARs do not appear to covary

during the Holocene (Fig. 9). Other dissolution indicators (e.g., % benthics and % planktic foraminiferal fragments) are not correlated with the NPG and BFAR. Furthermore, there is no significant correlation (Table 3) or direct correspondence between increases or decreases in NPG and increases or decreases in sediment AR, suggesting that the NPG fluctuations are caused by productivity changes of benthic foraminifera and not by variations in the dilution of the benthic foraminifera with terrigenous material or planktic foraminifera. The only exceptions of good preservation are in the intervals 8.5-8.2 ka where the benthic foraminifera are poorly preserved and fragmented and at 10.3, 9.3 and 7.7 ka where samples contain some poorly preserved/fragmented benthic foraminifera; these periods are cold intervals (Bond et al., 1997, 2001; Mayeweski et al., 2004; Wanner et al. 2011, 2015).

The %, NPG and AR of 'phytodetritus species' are significantly correlated with the % coarse fraction, and weakly with % benthics and % planktic foraminiferal fragments. Variability in bottom currents during the Holocene may have been responsible to varying extents for winnowing the organic matter, or there may have been fluctuations in the extent of mid-water competition for food.

Comparing the AR of 'phytodetritus species' and the AR of benthic foraminifera calculated on a 'phytodetritus species' -free basis provides useful insights in the relative contribution of seasonally driven or more sustained fluxes of organic carbon, particularly in abyssal areas (Diz and Barker, 2016). The AR of 'phytodetritus species' compared with that of 'other' foraminifera (calculated on a 'phytodetritus species'-free basis) covary strongly throughout the Holocene, suggesting that most benthic foraminifera at this site are influenced by seasonal inputs of organic matter, although carbonate dissolution cannot be ruled out.

The BFAR values at ODP Site 980 (as estimated for DBD) over the last 12 kyr (mean 57529 cm^{-2} kyr^{-1}, n = 44, including zeros) are considerably higher than at nearby sites in the NE Atlantic, e.g., at Biogeochemical Ocean Flux Studies (BOFS) cores 5K (50°N, 21°W, water depth 3547 m; mean 1583 cm^{-2} kyr^{-1}, n = 66)) and 14K (58°N, 19°W, water depth 1756 m, mean 8152 cm^{-2} kyr^{-1}, n = 36) (Thomas et al.,

1995), and core 13078#16 (48°49.91 N, 16°29.94 W, water depth 4844 m; mean 1135 cm^{-2} kyr^{-1}, n = 41) (Smart, 2008) (Fig. 1, Fig. 10c). This difference remains when BFARs are scaled with water depth (i.e., calculated as BFAR multiplied by water depth, BFAR*Z) (Herguera and Berger, 1991) (Fig. 10d). The NPG, however, at ODP Site 980, are generally lower than at BOFS cores 5K and 14K ,and higher than core 13078#16.

The higher BFARs at ODP Site 980 as compared with those at the nearby sites are thus due to the higher sedimentation rates in the Feni Drift region, and indicate that in general organic matter was not removed significantly from the site. The peaks in BFARs might reflect times of increased lateral current transport bringing in organic matter, or even transported benthic foraminifera. We think the latter option less probable because the foraminifera do not show evidence of transportation, but are – on the contrary – well preserved, unabraded, and not size-sorted. Regional differences in productivity, as reflected in the BFARs, could be linked to the position of the Arctic Front (AF), which may have varied and reached the area of Site 980 during Holocene cold intervals, as it did during cold intervals close to the end of the last interglacial (MIS5) (Mokeddem et al., 2014).

There is no straightforward relationship between the Site 980 benthic foraminiferal faunas and the benthic foraminiferal stable isotope records (Oppo et al., 2003, 2007). Using benthic $\delta^{13}C$ values, Oppo et al. (2003) suggested that significant changes occurred in NADW formation during the Holocene at Site 980. They recognised reductions of NADW (as recognized by decreases in benthic foraminiferal $\delta^{13}C$) at 9.3 ka, 8.0 ka, 5.0 ka and 2.8 ka (Fig. 2), with a decreasing trend of NADW beginning at 6.5 ka. General decreases in the NPG and BFAR coincide with intervals of reduced NADW.

Only small variations occur in benthic $\delta^{18}O$ values throughout the studied interval, with more positive values at 12-11.5 ka (Younger Dryas). During the Younger Dryas, the intensity of Atlantic meridional overturning circulation (AMOC) decreased (e.g., Boyle and Keigwin, 1987; Evans and Hall,

2008; Lynch-Stieglitz et al. 2011). The % abundance of *S. fusiformis* was higher during and following the Younger Dryas compared with the rest of the Holocene.

The increased % of *S. fusiformis* following and during the Younger Dryas is not reflected in higher AR of *S. fusiformis* or BFARs, suggesting export productivity was low, at highly variable conditions. During this interval, the so-called 'H10 species' (*T. pauperata*, *S. fusiformis* and *A. weddellensis*) had higher % abundances, which may suggest that they are all opportunistic species, although at lower verall export productivity (as reflected in low BFARs). The position of the Arctic Front (AF) may have shifted southwards reaching the area of Site 980 during the Younger Dryas, as it did during cold intervals of the last interglacial (MIS5) (Mokeddem et al., 2014). The % of ice-rafted debris (IRD) at Site 980 was higher during the Younger Dryas (McManus et al., 1999, 2004), thus the site may have had some ice cover, so phytodetritus blooms were less prevalent and, as a consequence, the non-phytodetritus taxa had higher percentages. Ice cover could have affected the type of phytodetrital delivery to the seafloor, or possibly phytodetritus was more concentrated in shorter time periods, affecting the benthic foraminiferal assemblage in favour of the 'H10 species'.

We find no straightforward relationship between the benthic foraminiferal faunal fluctuations at ODP Site 980 and the so-called Bond cycles (Bond et al., 1997, 2001), keeping in mind there is no consensus of opinion as to whether the Bond cycles actually exist (e.g. Wunsch, 2000; Wanner et al. 2008; Obrochta et al., 2012). Increases in carbonate dissolution, reflected in decreases in the NPG, BFAR and % coarse fraction, and poorly preserved/fragmented benthic foraminifera occur during the '8.2 ka cold event' which has been linked to reduced Atlantic meridional overturning circulation due to freshwater pulses from the melting Laurentide ice sheet (e.g. Kleiven et al. 2008; Wiersma et al. 2011). Samples from other cold intervals at 10.3, 9.3 and 7.7 ka also contain some poorly preserved/fragmented benthic foraminifera (Bond et al., 1997, 2001; Mayeweski et al., 2004; Wanner et al. 2011, 2015). Yasuhara et al. (2014) suggested that the diversity of deep-sea ostracods and foraminifera in the North Atlantic over the last 20 kyr is linked to changes in AMOC variability (specifically bottom-water temperature), with increased

diversity during Heinrich 1, the Younger Dryas and the 8.2 ka event. We did not find a simple relationship between benthic foraminiferal diversity changes (alpha index) and potential AMOC variability (reflected in benthic $\delta^{13}C$ values, Oppo et al., 2003), bottom-water temperature (broadly reflected in $\delta^{18}O$ values, Oppo et al., 2003, 2007) and Bond cycles. In our data, however, alpha diversity was high during the low abundance interval of the Younger Dryas.

7. Conclusions

(1) The absolute and relative abundances and diversity of benthic foraminifera varied significantly during the Holocene (last 12 kyr) at bathyal ODP Site 980.

(2) Peaks in the relative abundance of 'phytodetritus species' (combined % of *N. iridea*, *A. weddellensis*, *C. obtusa*, and rare *E. exigua*) occurred at 8.0 ka, 7.0 ka, 6.3-5.6 ka, 4.7 ka, 4.3-3.4 ka and 2.4 ka. These peaks generally correspond to peaks in absolute abundance (number of specimens per gram, accumulation rate) indicating that these are intervals of increases in the seasonality of productivity.

(3) The absolute and relative abundance of 'phytodetritus species' did not covary during the Holocene, suggesting that they have different ecological requirements.

(4) There appears to be no simple relationship between changes in seasonality of export productivity and palaeoclimatic/palaeoceanographic records, such as variations in AMOC and the so-called Bond cycles.

(5) Bentho-pelagic coupling to local surface productivity might not be straightforward in a sediment drift setting, and it may have changed over time, e.g. through changes in the composition of planktonic ecosystems and/or current intensity. We speculate that currents at some times winnowed and removed fine-grained organic matter, so that it was not available to the benthic organisms, or that there may have been changes in mid-water competition for food, interfering with food fluxes to the seafloor.

(6) Between 11.7-10.8 ka (following the Younger Dryas), the % opportunistic species *S. fusiformis* increased, but not its AR, or BFARs, signifying surface productivity was low at highly fluctuating conditions, but the low overall BFARs may also have been caused by increased winnowing of organic material.

(7) Between ~12-10 ka, *A. weddellensis*, *S. fusiformis* and *T. pauperata* (so-called 'H10 species') had higher % abundances, and *B. difformis*, *C. laevigata*, *C. obtusa*, *E. vitrea* and *N. iridea* had lower % abundance (so-called 'L10 species').

(8) During the '8.2 ka cold event' and possibly less pronounced cold events carbonate dissolution increased.

(9) Overall, the benthic foraminiferal faunas at ODP Site 980 reflect highly dynamic conditions in export productivity and arrival of organic matter at the seafloor during the Holocene.

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Appendix A. Benthic foraminiferal taxonomic list

The benthic foraminiferal species mentioned in the text, including original names, are listed below.

Alabaminella weddellensis (Earland) = *Eponides weddellensis* Earland, 1936.

Bolivina difformis (Williamson) = *Textularia variabilis* var. *difformis* Williamson, 1858.

Cassidulina obtusa Williamson, 1858.

Cassidulina laevigata d'Orbigny, 1826.

Eilohedra vitrea (Parker) = *Epistominella vitrea* Parker, 1953.

Epistominella exigua (Brady) = *Pulvinulina exigua* Brady, 1884.

Nonionella iridea Heron-Allen and Earland, 1932.

Stainforthia fusiformis (Williamson) = *Bulimina pupoides* d'Orbigny var. *fusiformis* Williamson, 1858.

Trifarina pauperata (Heron-Allen and Earland) = *Uvigerina angulosa* Williamson var. *pauperata* Heron-Allen and Earland, 1932.

TABLES

Table 1. List of samples, ages and number of foraminifera studied from ODP Hole 980B. Shaded samples contained too few benthic foraminifera to be included in the % calculations.

Table 2. Top 10 ranked species (in all samples) in ODP Hole 980B.

Table 3. Correlation coefficients (*r*) and significance (*p*) values of species and other variables discussed in text in ODP Hole 980B.

Table 4. Correlation coefficients (*r*) and significance (*p*) values of species and other variables discussed in text in ODP Hole 980B.

FIGURES

Fig. 1. Location of ODP Site 980, NE Atlantic Ocean, and of other sites mentioned in text: BENBO Site C (Gooday and Hughes, 2002), BOFS cores 5K and 14K (Thomas et al., 1995) and BENGAL core 13078#16 (Smart, 2008). (a) Surface currents are shown as dashed arrows and red text (red = warm subtropical waters, orange = cool subpolar waters); NAC = North Atlantic Current, NC = Norwegian Current, SPG = subpolar gyre, STG = subtropical gyre. Deep water currents are shown as blue solid arrows and blue text (LSW: Labrador Sea Water, ISOW: Iceland-Scotland Overflow Water, EBDW: Eastern Basin Deep Water). Satellite-derived estimates of North Atlantic mean annual productivity (g C m^{-2} $year^{-1}$) based on SeaWiFS observations (Sun et al., 2006, fig. 3a; Corliss et al., 2009, fig. 1A). (b) Bathymetry of the NE Atlantic showing location of sites (modified after Lampitt et al., 2001 and Smart, 2008).

Fig. 2. (a) Benthic $\delta^{18}O$ records for ODP Hole 980B (left axis) (Oppo et al., 2003, 2007) compared with oxygen isotope data from the Greenland Ice Sheet Project 2 (GISP2) ice core (right axis) (Dansgaard et al., 1993; deMenocal, 2001, fig. 2A), (b) benthic $\delta^{13}C$ records for ODP Hole 980B (Oppo et al., 2003, 2007), (c) Percentage of lithic grains (ice-rafted debris, 63-150 μm size range) from stack of cores MC52-V29191+MC21-GGC22 (4 records) showing North Atlantic Bond events (numbered) (Bond et al., 2001, fig. 2). Shading in (b) shows low $\delta^{13}C$ events and possible correlative events in the other records; rectangles, denote extreme winter-like conditions from GISP2 (Oppo et al., 2003, fig 1; O'Brien, et al. 1995).

Fig. 3. Age-depth plot, sediment accumulation rate (cm/kyr), % weight >63 μm size-fraction, % planktic foraminiferal fragments and % benthic foraminifera in ODP Hole 980B. Arrows in (e) indicate samples that contained no or too few benthic foraminifera (0-13 specimens) to be used for percentage calculations (shown by gaps in the record).

Fig. 4. Number of specimens per gram (NPG), NPG of 'phytodetritus species' (sum of *N. iridea*, *A. weddellensis*, *C. obtusa*, and *E. exigua*), % 'phytodetritus species', % of individual 'phytodetritus species', benthic foraminiferal accumulation rates (BFAR), accumulation rates (AR) of 'phytodetritus species', AR of benthic foraminifera calculated on a 'phytodetritus species'-free basis, and alpha index in ODP Hole 980B. ARs were calculated using WBD data (all data points included). Gaps in the % and alpha index records indicate samples that contained no or too few benthic foraminifera (0-13 specimens) to be used for percentage calculations. Arrows in (c) show peaks in 'phytodetritus species' (>45%, dashed horizontal line), and arrows in (e) show peaks in BFARs (>200,000 cm^{-2} kyr^{-1}).

Fig. 5. Relative abundances (%) of the most common species in ODP Hole 980B. Gaps in the % records indicate samples that contained no or too few benthic foraminifera (0-13 specimens) to be used for percentage calculations.

Fig. 6. Absolute abundances (AR, accumulation rates – number of specimens cm^{-2} kyr^{-1}) of the most common species in ODP Hole 980B. ARs were calculated using WBD data (all data points included).

Fig. 7. (a) Relative abundances of 'H10 species' (i.e., species with higher % abundance before 10 ka) (combined % of *A. weddellensis*, *S. fusiformis* and *T. pauperata*), and 'L10 species' (i.e., species with lower % abundance before 10 ka) (combined % of *B. difformis*, *C. laevigata*, *C. obtusa*, *E. vitrea* and *N. iridea*). Gaps in the % records indicate samples that contained no or too few benthic foraminifera (0-13 specimens) to be used for percentage calculations. ARs were calculated using WBD data (all data points included).

Fig. 8. (a) Comparison between BFARs (total) and accumulation rates of 'high food species' (sum of *Abditodentrix* spp., *Bolivina* spp., *Bolivinellina* spp., *Brizalina* spp., *Bulimina* spp., *Globobulimina* spp., *Melonis* spp. *Stainforthia* spp., *T. pauperata* and *Uvigerina* spp.), (b) relative abundances (%) of 'high food species', and (c) % of 'high food species' calculated on a 'phytodetritus species'-free basis in ODP Hole 980B. ARs were calculated using WBD data (all data points included). Gaps in the % records indicate samples that contained no or too few benthic foraminifera (0-13 specimens) to be used for percentage calculations.

Fig. 9. Comparison between (a) BFARs (calculated using WBD data), and (b) coccolith accumulation rates (AR, calculated using WBD data) (modified after Berger et al., 2014, fig. 10c) in ODP Site 980. Arrows in (a) show peaks in BFARs (>200,000 cm^{-2} kyr^{-1}).

Fig. 10. (a) Comparisons of BFARs between ODP Hole 980B (calculated using wet bulk density, WBD), BOFS cores 5K and 14K (Thomas et al., 1995), and BENGAL core 13078#16 (Smart, 2008). Note logarithmic scale. (b) Comparisons of BFAR*Z index (calculated as BFAR multiplied by water depth, Herguera and Berger, 1991) between ODP Hole 980B (calculated using WBD), BOFS cores 5K and 14K (Thomas et al., 1995), and BENGAL core 13078#16 (Smart, 2008). Note logarithmic scale. (c) and (d) same as (a) and (b) respectively, apart from BFARs in ODP Hole 980B were calculated using estimated dry bulk densities (DBD).

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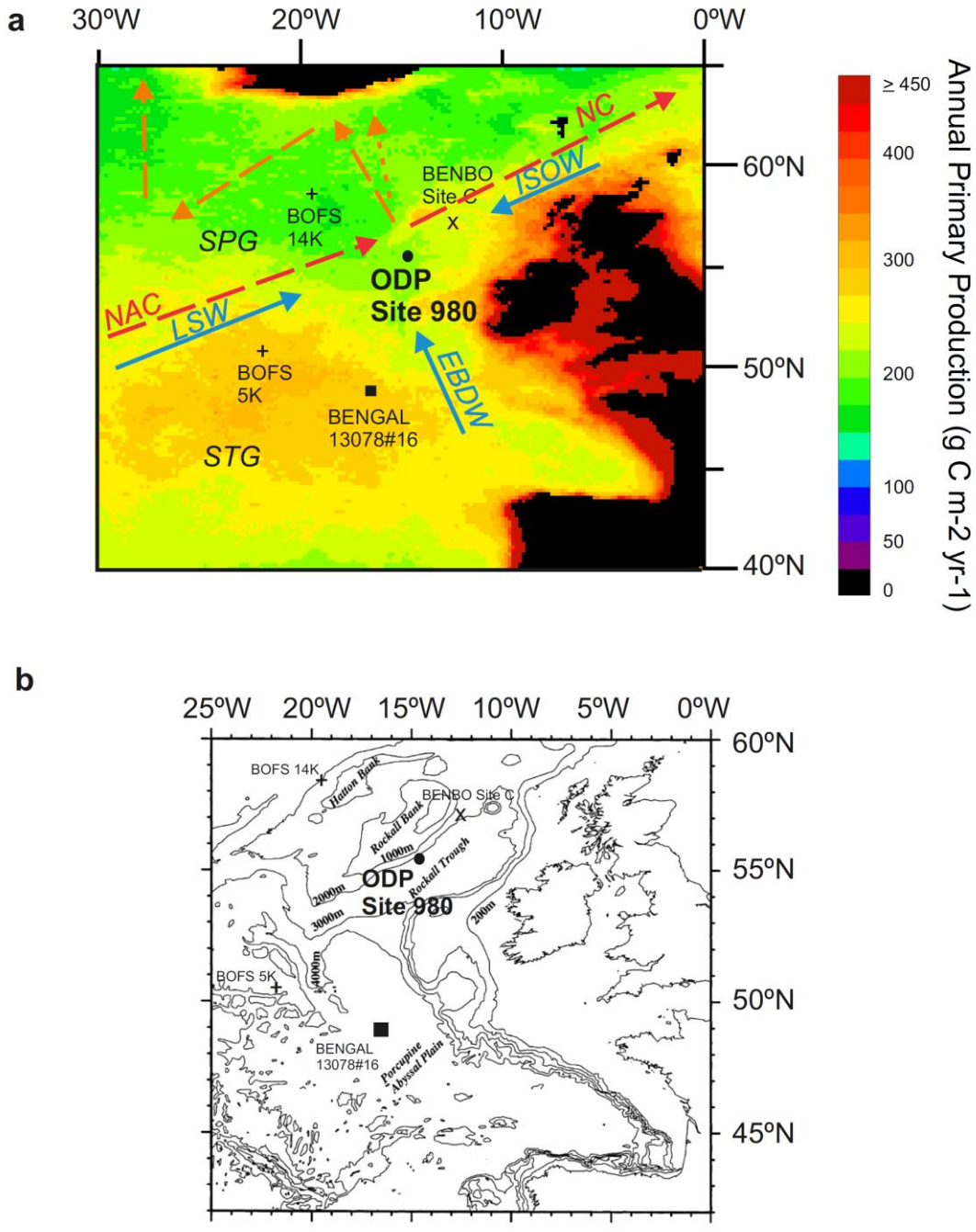

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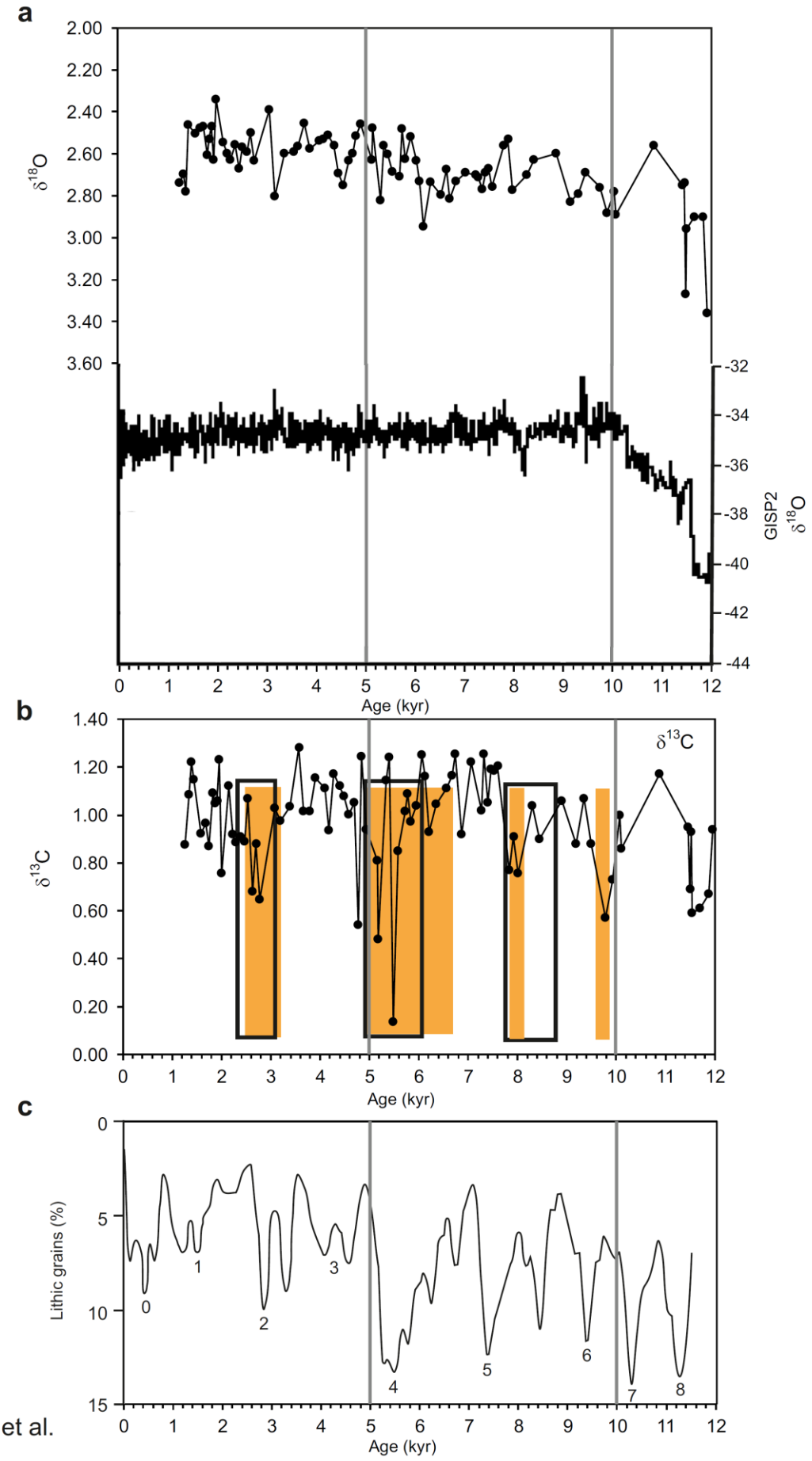

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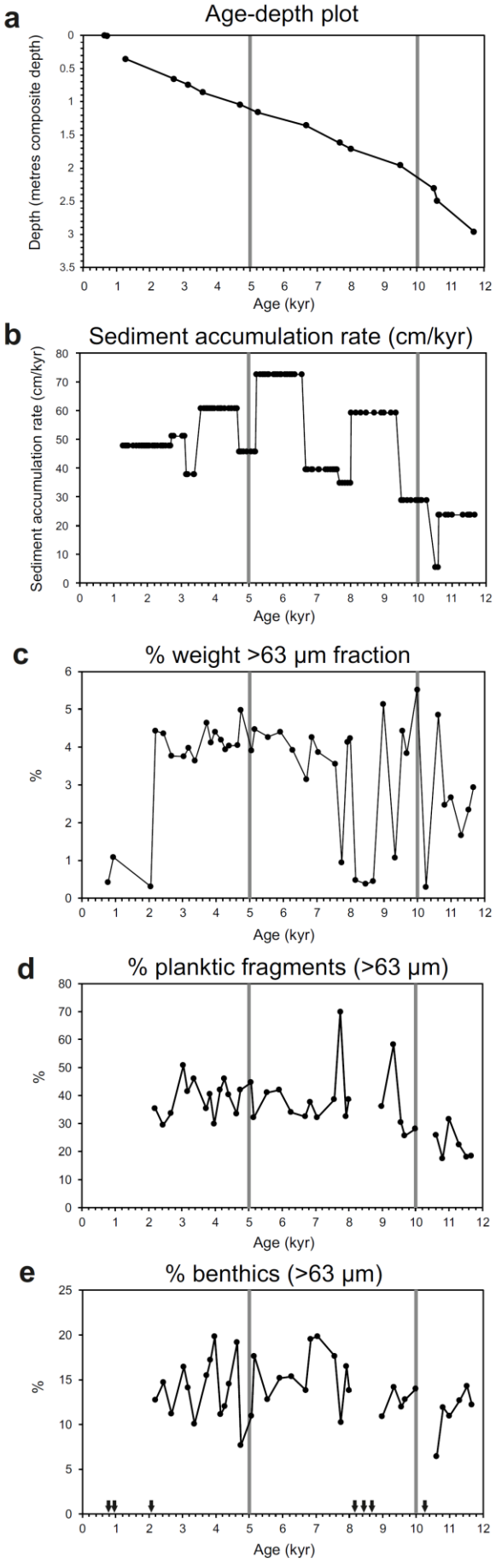

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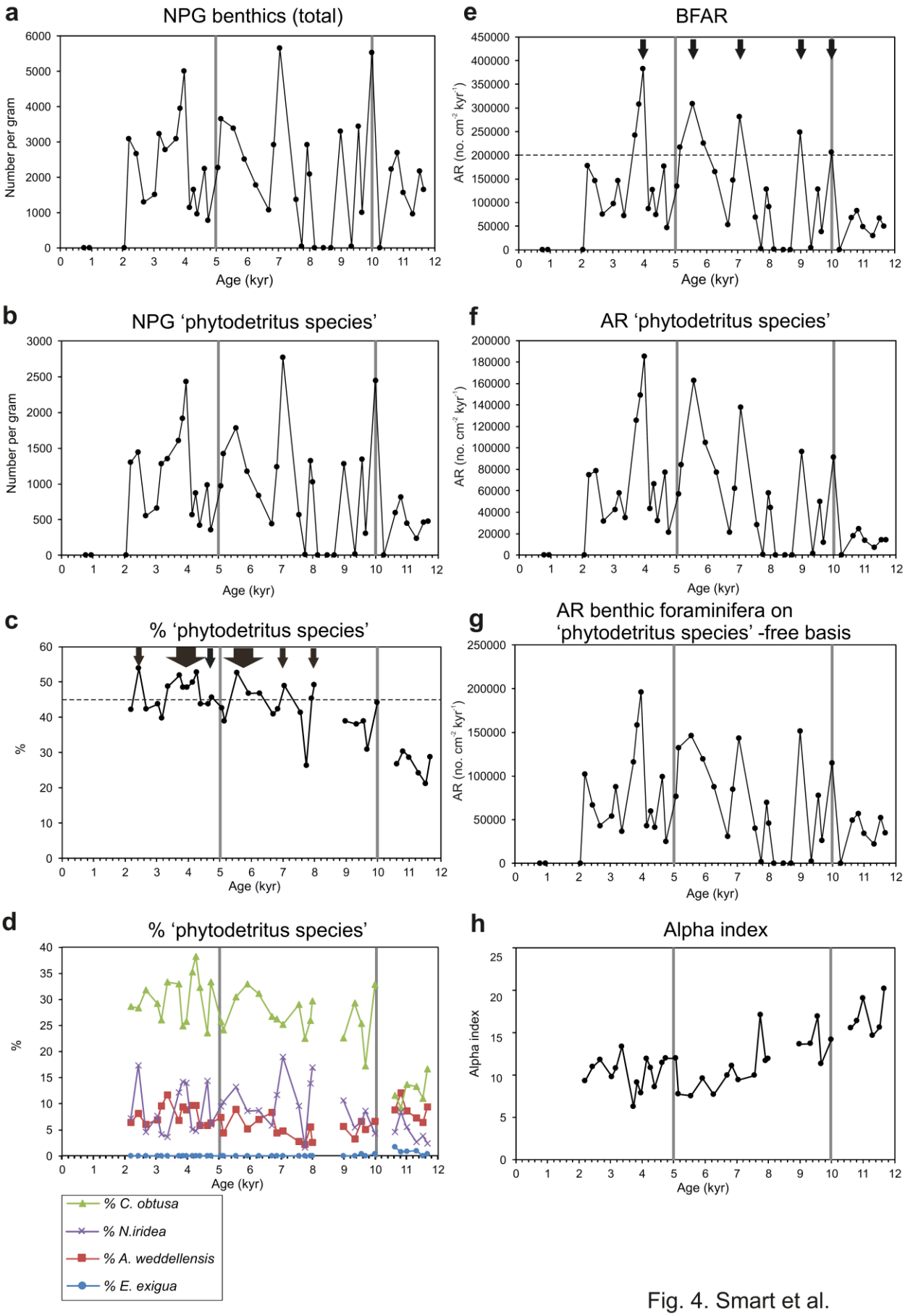

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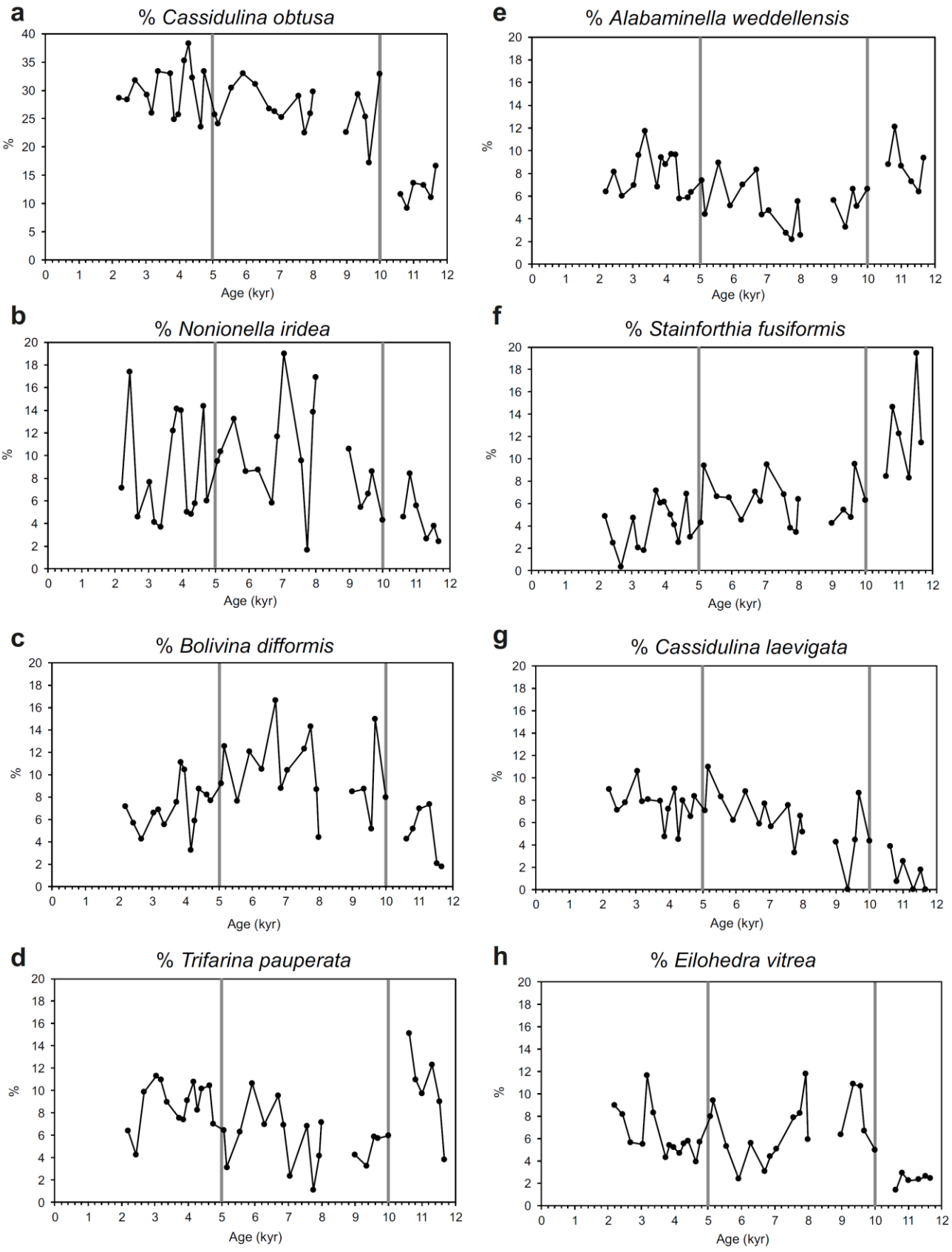

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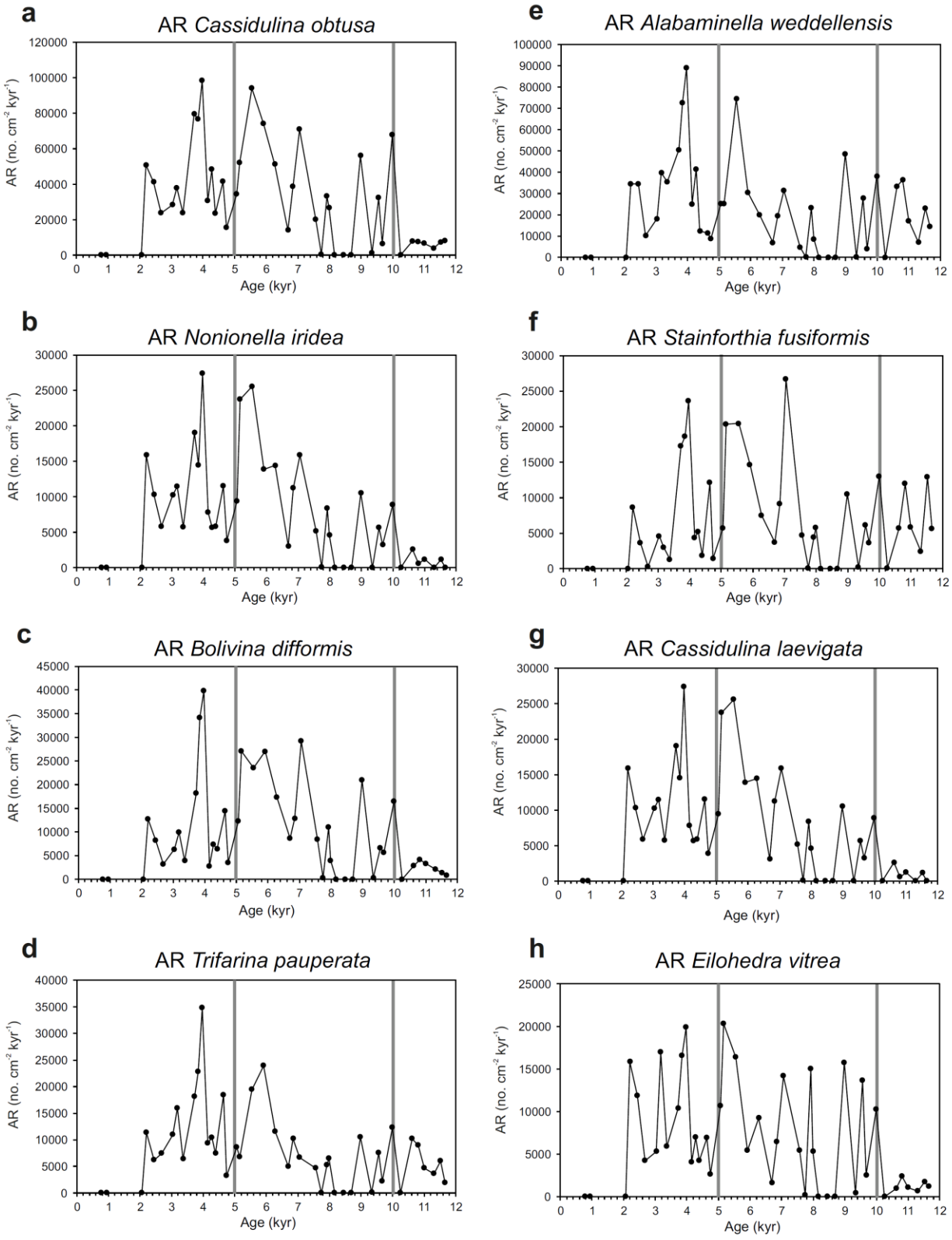

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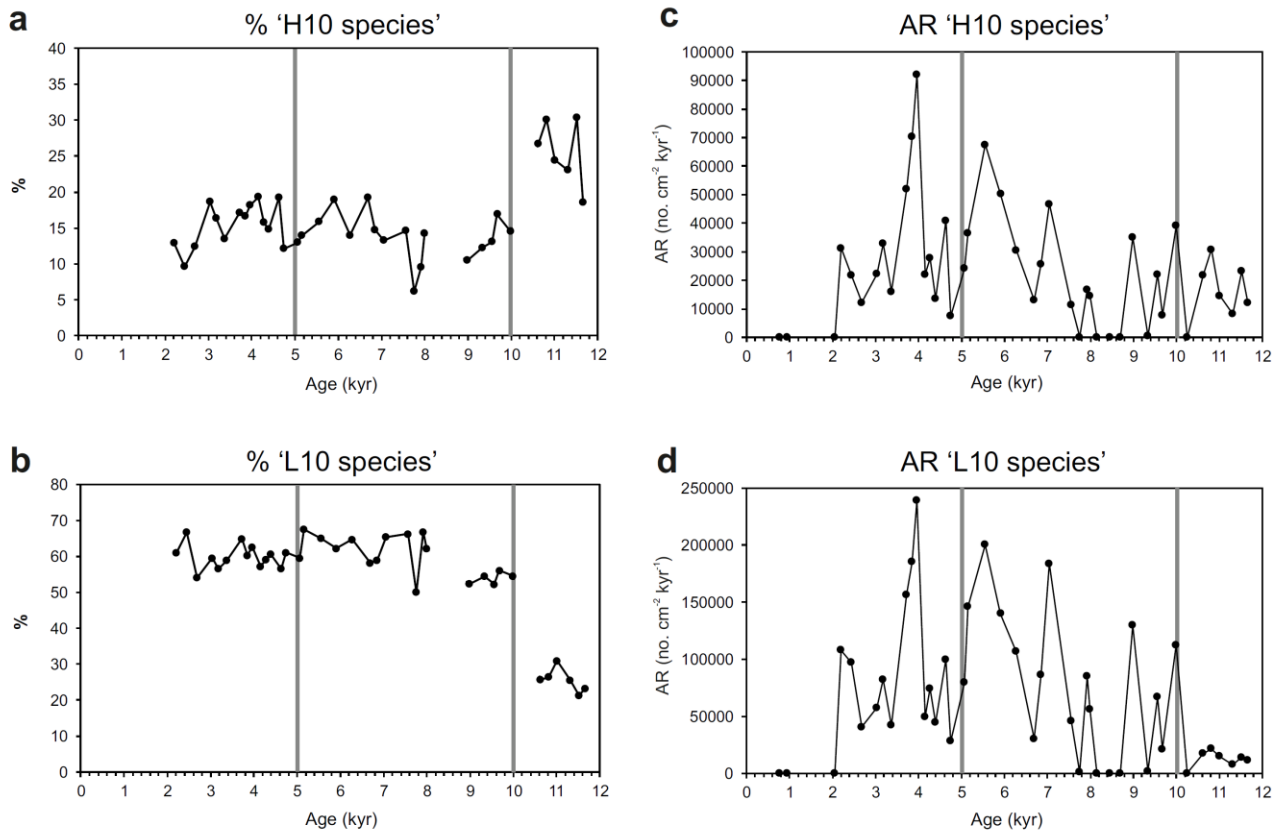

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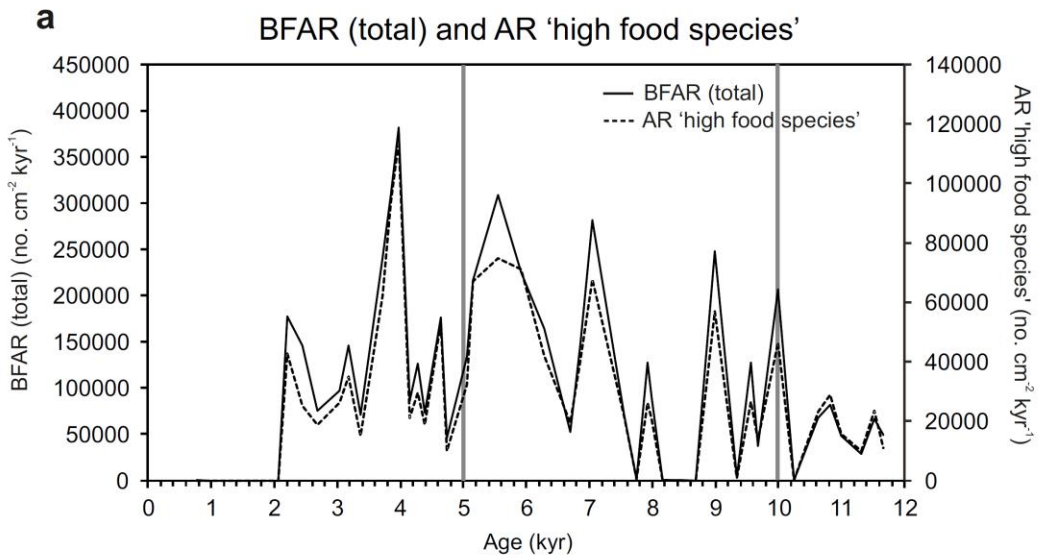

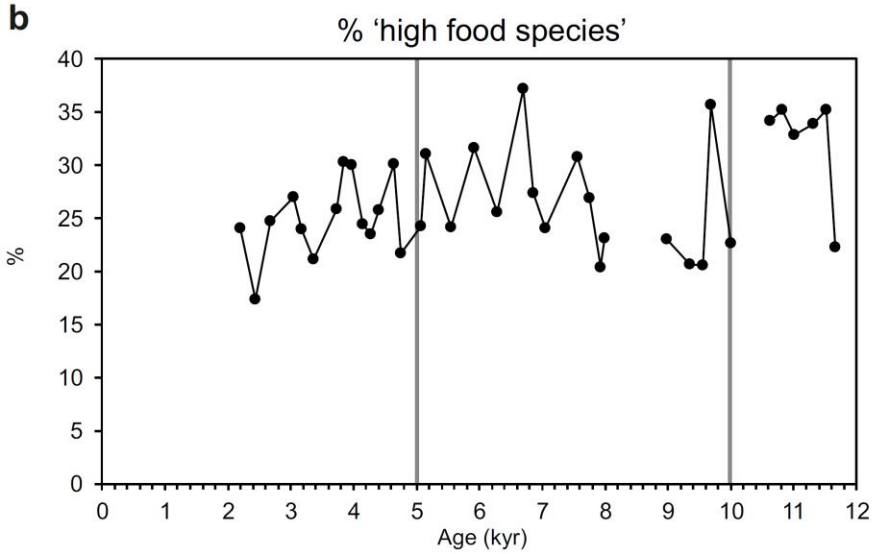

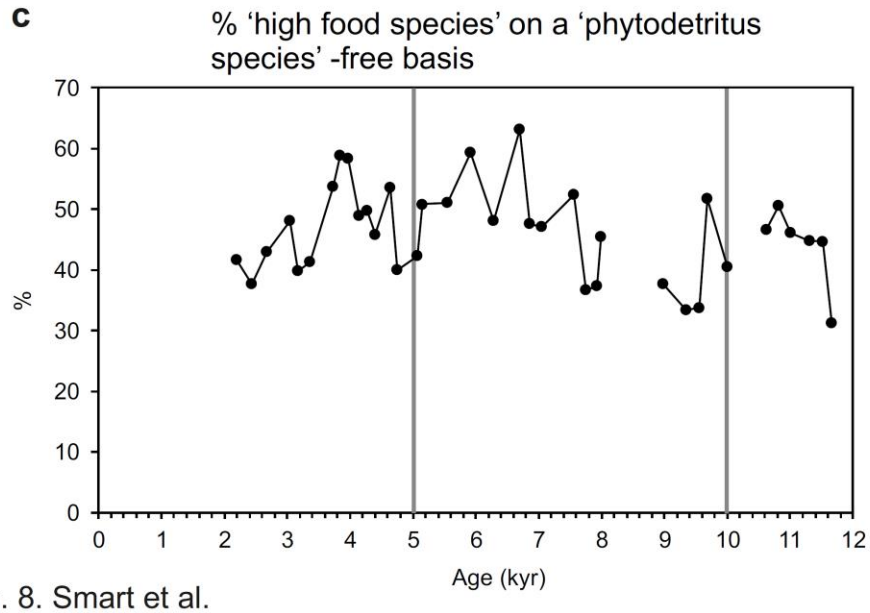

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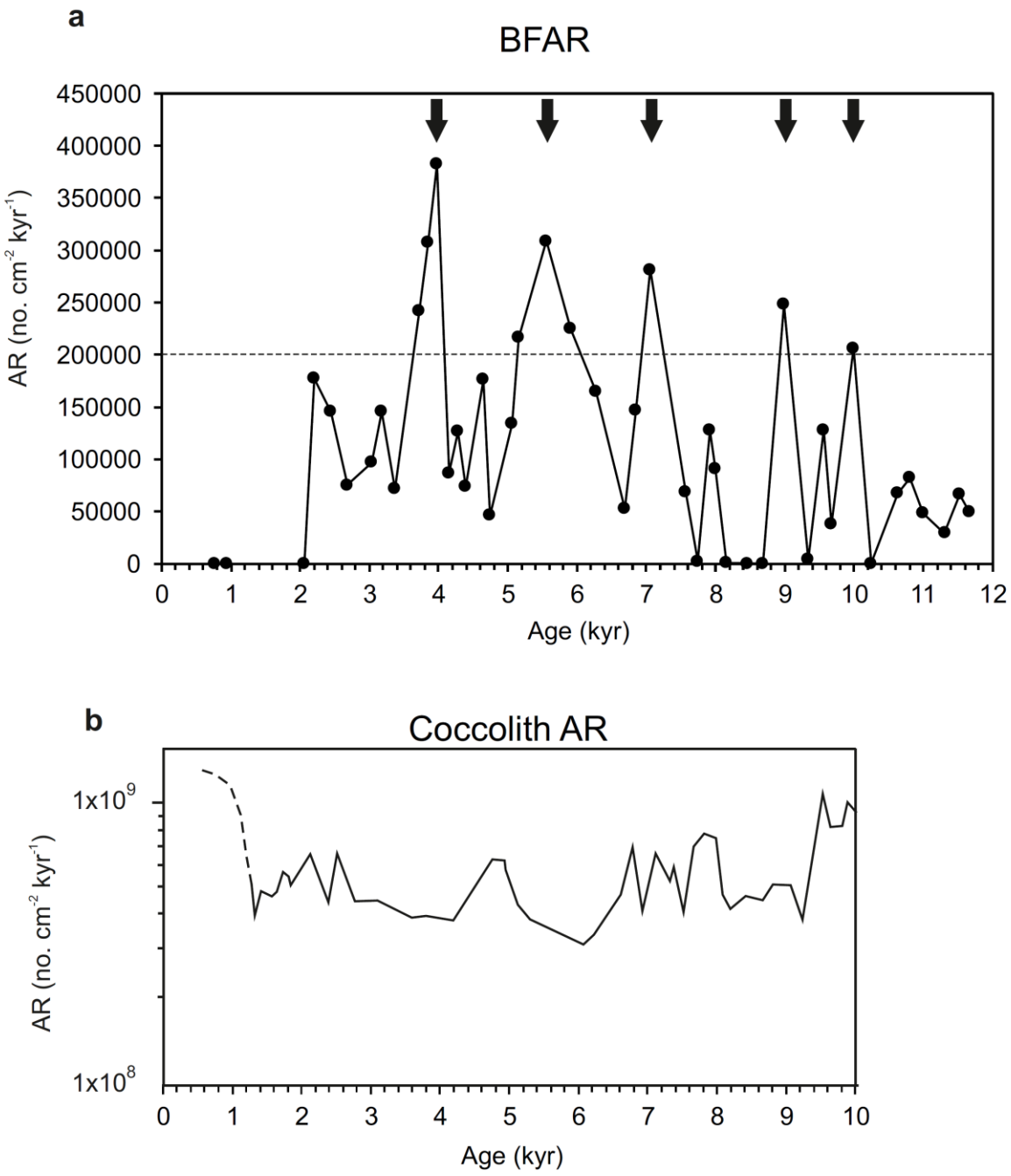

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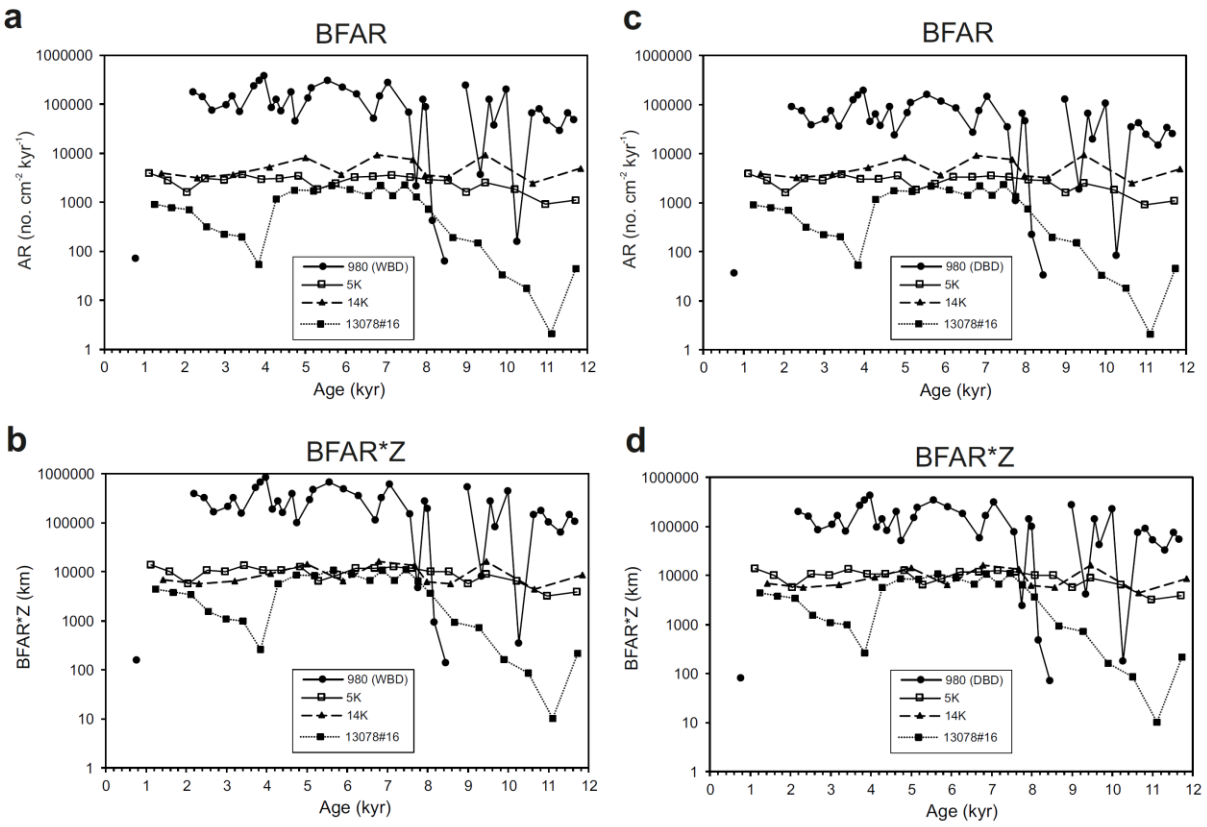

Fig. 10. Smart et al.

Table 1. Smart et al.

Sample (Site-core-section, interval [cm])	Metres composite depth (mcd)	Age (kyr)	Total no. benthic foraminifera counted
980B-1H-1, 4-5	0.045	0.78	6
980B-1H-1, 15-16	0.155	0.95	0
980B-1H-1, 52-53	0.525	2.06	0
980B-1H-1, 55-56	0.555	2.20	391
980B-1H-1, 60-61	0.605	2.44	282
980B-1H-1, 65-66	0.655	2.68	283
980B-1H-1, 72-73	0.725	3.04	274
980B-1H-1, 75-76	0.755	3.18	292
980B-1H-1, 80-81	0.805	3.37	435
980B-1H-1, 88-89	0.885	3.73	279
980B-1H-1, 90-91	0.905	3.85	297
980B-1H-1, 92-93	0.925	3.97	307
980B-1H-1, 95-96	0.955	4.15	278
980B-1H-1, 97-98	0.975	4.27	290
980B-1H-1, 99-100	0.995	4.40	276
980B-1H-1, 103-104	1.035	4.64	306
980B-1H-1, 105-106	1.055	4.75	300
980B-1H-1, 112-113	1.125	5.07	326
980B-1H-1, 114-115	1.145	5.16	319

980B-1H-1, 120-121	1.205	5.55	302
980B-1H-1, 125-126	1.255	5.91	291
980B-1H-1, 130-131	1.305	6.28	286
980B-1H-1, 136-137	1.365	6.69	325
980B-1H-1, 140-141	1.405	6.85	274
980B-1H-1, 145-146	1.455	7.05	337
980B-1H-2, 8-9	1.585	7.56	293
980B-1H-2, 13-14	1.635	7.75	182
980B-1H-2, 18-19	1.685	7.92	289
980B-1H-2, 20-21	1.705	7.99	390
980B-1H-2, 23-24	1.735	8.16	13
980B-1H-2, 28-29	1.785	8.45	2
980B-1H-2, 32-33	1.825	8.69	0
980B-1H-2, 37-38	1.875	8.99	283
980B-1H-2, 43-44	1.935	9.34	92
980B-1H-2, 48-49	1.985	9.56	272
980B-1H-2, 52-53	2.025	9.68	314
980B-1H-2, 63-64	2.135	10.00	301
980B-1H-2, 72-73	2.225	10.25	10
980B-1H-2, 100-101	2.505	10.62	284
980B-1H-2, 108-109	2.585	10.81	273
980B-1H-2, 116-117	2.665	11.00	359
980B-1H-2, 129-130	2.795	11.31	301
980B-1H-2, 138-139	2.885	11.52	344

980B-1H-2, 144-145	2.945	11.66	288

Table 2. Smart et al.

Rank	**Species**	**%**
1	*Cassidulina obtusa*	25.8
2	*Nonionella iridea*	8.6
3	*Bolivina difformis*	8.0
4	*Trifarina pauperata*	7.7
5	*Alabaminella weddellensis*	7.0
6	*Stainforthia fusiformis*	6.5
7	*Cassidulina laevigata*	6.1
8	*Eilohedra vitrea*	5.8
9	*Astrononion stelligerum*	3.0
10	*Cibicidoides* sp. 1 (juvenile)	1.8

Table 3. Smart et al.

		Diversity (alpha index)	NPG	BFAR	Sed. rate (cm/kyr)	% Benthics	% Planktic fragments	% Wt. >63 µm fraction	% 'Phytodetritus species'	NPG 'Phytodetritus species'	AR 'Phytodetritus species'	'High food species' (% of total)	'High food species' (on 'phytodetritus species' -free basis)
Diversity (alpha index)	*r*	1	-0.266	**-0.583**	**-0.714**	**-0.538**	-0.196	**-0.459**	**-0.710**	-0.417	**-0.629**	0.039	**-0.575**
	p		0.111	<0.001	<0.001	0.001	0.246	0.004	<0.001	0.010	<0.001	0.820	<0.001
	n	37	37	37	37	37	37	37	37	37	37	37	37
NPG	*r*	-0.266	1	**0.872**	0.086	**0.437**	-0.328	**0.739**	0.356	**0.972**	**0.828**	-0.150	0.142
	p	0.111		<0.001	0.581	0.007	0.047	<0.001	0.031	<0.001	<0.001	0.375	0.402
	n	37	44	44	44	37	37	44	37	44	44	37	37
BFAR	*r*	**-0.583**	**0.872**	1	**0.450**	**0.527**	-0.096	**0.699**	**0.559**	**0.908**	**0.988**	-0.109	0.397
	p	<0.001	<0.001		0.002	0.001	0.570	<0.001	<0.001	<0.001	<0.001	0.520	0.015
	n	37	44	44	44	37	37	44	37	44	44	37	37
Sed. rate (cm/kyr)	*r*	**-0.714**	0.086	**0.450**	1	0.291	**0.444**	0.220	**0.697**	0.212	**0.502**	-0.246	0.366
	p	<0.001	0.581	0.002		0.080	0.006	0.152	<0.001	0.167	0.001	0.143	0.026
	n	37	44	44	44	37	37	44	37	44	44	37	37
% Benthics	*r*	**-0.538**	**0.437**	**0.527**	0.291	1	-0.073	0.092	0.337	**0.489**	**0.525**	0.088	0.412
	p	0.001	0.007	0.001	0.080		0.670	0.588	0.041	0.002	0.001	0.606	0.011
	n	37	37	37	37	37	37	37	37	37	37	37	37
% Planktic fragments	*r*	-0.196	-0.328	-0.096	**0.444**	-0.073	1	-0.194	0.308	-0.169	-0.026	-0.358	-0.109
	p	0.246	0.047	0.570	0.006	0.670		0.249	0.064	0.317	0.880	0.029	0.519
	n	37	37	37	37	37	37	37	37	37	37	37	37
% Wt. >63 µm fraction	*r*	**-0.459**	**0.739**	**0.699**	0.220	0.092	-0.194	1	**0.586**	**0.720**	**0.658**	-0.273	0.178
	p	0.004	<0.001	<0.001	0.152	0.588	0.249		<0.001	<0.001	<0.001	0.102	0.293
	n	37	44	44	44	37	37	44	37	44	44	37	37
% 'Phytodetritus species'	*r*	**-0.710**	0.356	**0.559**	**0.697**	0.337	0.308	**0.586**	1	**0.561**	**0.645**	**-0.542**	0.256
	p	<0.001	0.031	<0.001	<0.001	0.041	0.064	<0.001		<0.001	<0.001	0.001	0.127
	n	37	37	37	37	37	37	37	37	37	37	37	37
NPG 'Phytodetritus species'	*r*	-0.417	**0.972**	**0.908**	0.212	**0.489**	-0.169	**0.720**	**0.561**	1	**0.897**	-0.268	0.193

	p	0.010	<0.001	<0.001	0.167	0.002	0.317	<0.001	<0.001		<0.001	0.109	0.252
	n	37	44	44	44	37	37	44	37	44	44	37	37
AR 'Phytodetritus species'	*r*	**-0.629**	**0.828**	**0.988**	**0.502**	**0.525**	-0.026	**0.658**	**0.645**	**0.897**	1	-0.163	0.415
	p	<0.001	<0.001	<0.001	0.001	0.001	0.880	<0.001	<0.001	<0.001		0.335	0.011
	n	37	44	44	44	37	37	44	37	44	44	37	37
'High food species' (% of total)	*r*	0.039	-0.150	-0.109	-0.246	0.088	-0.358	-0.273	**-0.542**	-0.268	-0.163	1	**0.667**
	p	0.820	0.375	0.520	0.143	0.606	0.029	0.102	0.001	0.109	0.335		<0.001
	n	37	37	37	37	37	37	37	37	37	37	37	37
'High food species' (on 'phytodetritus species' -free basis)	*r*	**-0.575**	0.142	0.397	0.366	0.412	-0.109	0.178	0.256	0.193	0.415	**0.667**	1
	p	<0.001	0.402	0.015	0.026	0.011	0.519	0.293	0.127	0.252	0.011	<0.001	
	n	37	37	37	37	37	37	37	37	37	37	37	37

In bold: correlation is significant at the 0.01 level (2-tailed).

Table 4. Smart et al.

		% *B. difformis*	% *E. vitrea*	% *A. weddellensis*	% *C. obtusa*	% *N.iridea*	NPG Benthics (on 'phytodetritus species' -free basis)	AR Benthics (on 'phytodetritus species' -free basis)
Diversity (alpha index)	*r*	**-0.421**	-0.179	0.131	**-0.592**	**-0.526**	-0.110	**-0.520**
	p	0.009	0.288	0.441	<0.001	0.001	0.516	0.001
	n	37	37	37	37	37	37	37
NPG	*r*	-0.017	0.062	0.185	0.046	**0.514**	**0.980**	**0.894**
	p	0.919	0.717	0.272	0.788	0.001	<0.001	<0.001
	n	37	37	37	37	37	44	44
BFAR	*r*	0.169	0.005	0.117	0.246	**0.637**	**0.802**	**0.989**
	p	0.317	0.978	0.492	0.142	<0.001	<0.001	<0.001
	n	37	37	37	37	37	44	44

Sed. rate (cm/kyr)	*r*	0.221	0.084	-0.034	**0.668**	0.330	-0.027	**0.392**
	p	0.189	0.623	0.843	<0.001	0.046	0.860	0.009
	n	37	37	37	37	37	44	44
% Benthics	*r*	0.346	0.091	-0.299	0.139	**0.617**	0.360	**0.515**
	p	0.036	0.591	0.072	0.413	<0.001	0.029	0.001
	n	37	37	37	37	37	37	37
% Planktic fragments	*r*	0.297	**0.433**	-0.318	**0.558**	-0.099	**-0.453**	-0.164
	p	0.074	0.007	0.055	<0.001	0.560	0.005	0.332
	n	37	37	37	37	37	37	37
% Wt. >63 µm fraction	*r*	-0.060	0.040	0.101	**0.423**	0.402	**0.723**	**0.722**
	p	0.723	0.815	0.553	0.009	0.014	<0.001	<0.001
	n	37	37	37	37	37	44	44
% 'Phytodetritus species'	*r*	0.067	0.249	0.076	**0.846**	**0.569**	0.144	**0.457**
	p	0.692	0.137	0.656	<0.001	<0.001	0.394	0.004
	n	37	37	37	37	37	37	37
NPG 'Phytodetritus species'	*r*	0.055	0.114	0.150	0.249	**0.612**	**0.906**	**0.899**
	p	0.746	0.500	0.376	0.137	<0.001	<0.001	<0.001
	n	37	37	37	37	37	44	44
AR 'Phytodetritus species'	*r*	0.175	0.009	0.123	0.334	**0.663**	**0.732**	**0.955**
	p	0.299	0.959	0.469	0.043	<0.001	<0.001	<0.001
	n	37	37	37	37	37	44	44
'High food species' (% of total)	*r*	0.347	**-0.575**	0.061	**-0.595**	-0.151	-0.032	-0.053
	p	0.035	<0.001	0.719	<0.001	0.372	0.850	0.757
	n	37	37	37	37	37	37	37
'High food species' (on 'phytodetritus species' -free basis)	*r*	**0.461**	**-0.465**	0.133	0.071	0.312	0.086	0.369
	p	0.004	0.004	0.431	0.675	0.060	0.613	0.025
	n	37	37	37	37	37	37	37

% *B. difformis*	*r*	1	0.167	-0.402	0.109	0.192	-0.083	0.158
	p		0.324	0.014	0.522	0.256	0.627	0.350
	n	37	37	37	37	37	37	37
% *E. vitrea*	*r*	0.167	1	-0.272	0.348	0.102	0.009	0.001
	p	0.324		0.103	0.035	0.548	0.957	0.997
	n	37	37	37	37	37	37	37
% *A. weddellensis*	*r*	-0.402	-0.272	1	-0.127	-0.204	0.206	0.107
	p	0.014	0.103		0.452	0.226	0.222	0.527
	n	37	37	37	37	37	37	37
% *C. obtusa*	*r*	0.109	0.348	-0.127	1	0.140	-0.144	0.152
	p	0.522	0.035	0.452		0.410	0.394	0.369
	n	37	37	37	37	37	37	37
% *N.iridea*	*r*	0.192	0.102	-0.204	0.140	1	0.391	**0.593**
	p	0.256	0.548	0.226	0.410		0.017	<0.001
	n	37	37	37	37	37	37	37
NPG Benthics (on 'phytodetritus species' -free basis)	*r*	-0.083	0.009	0.206	-0.144	0.391	1	**0.850**
	p	0.627	0.957	0.222	0.394	0.017		<0.001
	n	37	37	37	37	37	44	44
AR Benthics (on 'phytodetritus species' -free basis	*r*	0.158	0.001	0.107	0.152	**0.593**	**0.850**	1
	p	0.350	0.997	0.527	0.369	<0.001	<0.001	
	n	37	37	37	37	37	44	44

In bold: correlation is significant at the 0.01 level (2-tailed).